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Report

Attention Facilitates Multiple Stimulus Features in Parallel in Human Visual Cortex

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Summary

Successfully locating a dangerous or desirable object within a cluttered visual scene is a commonplace yet highly adaptive skill. In the laboratory, this ability is modeled by visual search experiments in which subjects try to find a target item surrounded by an array of distracting stimuli [1, 2]. Under certain conditions, targets that are distinguishable from distractors by virtue of having a particular combination of shared sensory features (e.g., a particular color and orientation) can be found rapidly regardless of the number of distractors [3, 4]. To explain this highly efficient localization of feature-conjunction targets, "guided search" theories [4–6] propose that attention is directed in parallel to the individual features that define the target, which then stands out from the distractors because of additive facilitation of its feature signals. Here we recorded frequency-tagged potentials evoked in human visual cortex and found that color and orientation features of target stimuli are indeed facilitated by attention in a parallel and additive manner. This additive feature-enhancement mechanism, reported here for the first time, not only enables rapid guided search but also plays a broader role in directing and sustaining attention to multi-feature objects and keeping them perceptually distinct from background clutter.

Results

In the present study, we investigated how attention was allocated to the individual features of targets (small, oriented bars) with a particular color and orientation in a factorial design. Subjects attended to these feature-conjunction targets in a visual display while ignoring equal numbers of randomly intermingled stimuli with only one or the other of the attended features or neither attended feature. The allocation of attention to each of the four stimulus types was assessed by means of noninvasive scalp recordings of steady-state visual-evoked potentials (SSVEPs). The SSVEP is the oscillatory potential field generated by visual cortical neurons in response to a flickering stimulus. Because the SSVEP has the same fundamental frequency as the driving stimulus, it is possible to record these frequency-coded responses concurrently from different stimuli that flicker at different rates within the same display. Importantly, the amplitude of the SSVEP is substantially increased when the driving stimulus is attended [7–10], thereby providing a sensitive measure of how strongly neural responses to each type of stimulus are amplified by attention in the visual cortex.

Informed consent was obtained from 15 subjects who observed a circular display containing 300 spatially intermingled isoluminant red and blue bars, half oriented vertically and half horizontally, which were continually moving in a jerky random fashion (Figure 1A). Frequency-coded SSVEPs were recorded separately and concurrently from the four types of bars (75 of each), which were flickered at different frequencies as follows: horizontal/blue = 10.00 Hz, vertical/red = 12.00 Hz, horizontal/red = 15.00 Hz, and vertical/blue = 17.14 Hz. Subjects attended to each of these dual-feature stimuli in turn on different runs. In this way the degree of sensory amplification could be obtained separately for each feature combination: (1) attended color and attended orientation (c^+o^+), (2) attended color and unattended orientation (c^+o^-), (3) unattended color and attended orientation (c^-o^+), and (4) unattended color and unattended location (c^-o^-).

Each trial began with a visual cue instructing which of the four types of bars (i.e., which feature combination) was to be attended. After cue offset, the display of flickering bars appeared. Subjects were instructed to maintain central fixation and to press a button whenever they detected occasional brief intervals (500 ms duration) of coherent motion of the bars with the attended color and orientation (the c^+o^+ targets). Similar coherent motion of the unattended bars (distractors) was to be ignored. Each trial lasted 3092 ms, and a total of 600 trials were presented. On a random 40% of the trials, one to three targets and/or distractors were presented. The SSVEPs were only analyzed on the remaining 60% of trials, with no coherent-motion targets or distractors. The amplitude of the frequency-tagged SSVEP to each stimulus type was quantified on each trial by means of fast Fourier transforms. The mean amplitudes over 11 occipital electrodes were normalized and statistically compared across stimulus types and attention conditions.

Attentional Effects on SSVEP Amplitudes

SSVEP waveforms were generally sinusoidal with fundamental frequencies at the driving flicker rate (Figure 1B). As in previous reports [8–11], SSVEP amplitudes were generally smaller for the higher flicker rates, but at each rate the amplitude was enlarged in response to stimuli with one or both of the attended features. Amplitudes were greatest for the attended conjunction (c^+o^+), intermediate for stimuli with one attended feature (c^+o^-, c^-o^+), and smallest for stimuli lacking either feature (c^-o^-) (Figures 2A and 3A). In the overall analysis of variance, SSVEP amplitudes were significantly enhanced for stimulus combinations with the attended versus unattended color ($p < 10^{-7}$) and the attended versus unattended orientation ($p < 0.001$). The interaction of color and orientation failed to reach significance, however ($p = 0.09$), indicating that the effects of attention on these two features were independently additive (Figure 3B). Further specific contrasts were calculated (two-tailed paired t tests, Bonferroni-Dunn corrected) to

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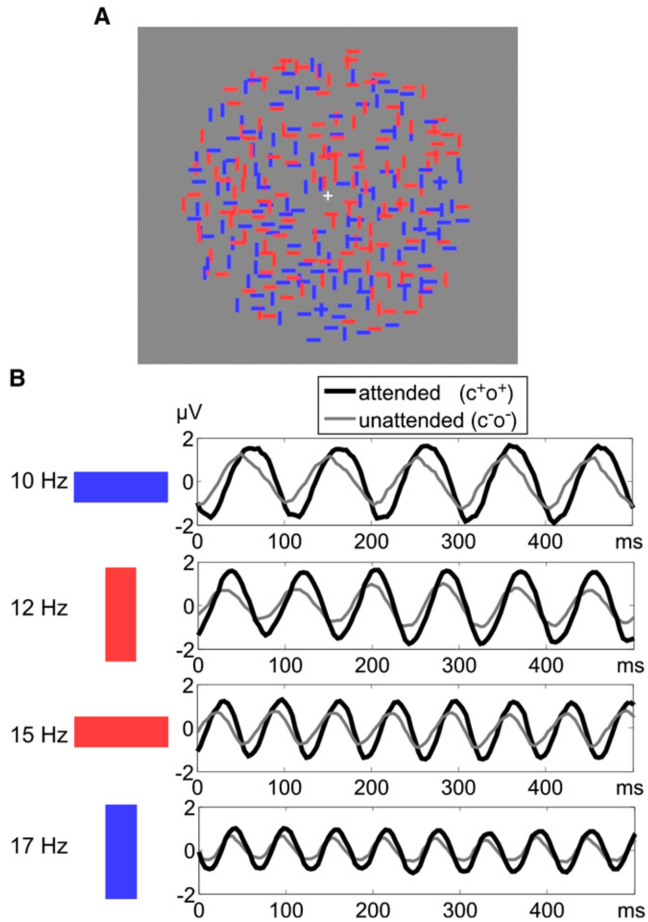

Figure 1. Stimulus Display and Typical SSVEP Waveforms

(A) Schematic diagram of the stimulus display, which had a diameter of 12.94° of visual angle. Individual bars extended 0.61° × 0.16° and moved 0.051° in a random direction with every frame of screen refresh (rate = 120 Hz).
(B) SSVEP waveforms from electrode Oz of a single subject averaged in the time domain with a moving window. Attended (c^+o^+) and unattended (c^-o^-) waveforms are depicted for each type of stimulus.

confirm the global effect of attending to color for stimuli with the unattended orientation (c^+o^- versus c^-o^-, $p < 10^{-7}$) and the global effect of attending to orientation for stimuli with the unattended color (c^-o^+ versus c^-o^-, $p < 0.005$).

Cortical Areas Showing SSVEP Modulation

For all four stimuli, SSVEP amplitudes had a tightly focused voltage maximum over the posterior occipital scalp (Figure 2B). To gain information about the cortical regions where sensory signals are amplified by feature-based attention, we localized cortical sources by means of variable-resolution electromagnetic tomography (VARETA [12]) and statistically compared between the c^+o^+ and c^-o^- conditions. As depicted in Figure 2C, the cortical currents giving rise to the SSVEP were localized to the posterior, medial occipital cortex. The Montreal Neurological Institute (MNI) coordinates [13] of the maximum modulations with attention averaged over the four stimuli were 12, 91, −12 for the right hemisphere and −21, 91, −14 for the left hemisphere. This occipital region, centered on the inferior lingual gyrus, includes early visual areas V1, V2, and V3.

Behavioral Results

Behavioral performance was generally high: the overall mean hit rate for detecting the coherent-motion targets was 86.5% ± 2.7%, with an average false-alarm rate of 3.7% ± 0.8%. False-alarm rates were higher in response to coherent-motion distractors that shared either color (4.3% ± 0.8%) or orientation (5.1% ± 1.4%) with the targets than to distractors that shared neither feature (1.6% ± 0.5%); both of these comparisons were significant (c^+o^- versus c^-o^-, $p < 0.001$; c^-o^+ versus c^-o^-, $p < 0.005$). False alarms did not differ between distractors sharing color and those sharing orientation (c^+o^- versus c^-o^+, $p > 0.1$).

Discussion

The SSVEP data reported here show that attending selectively to stimuli with a particular conjunction of color and orientation features facilitates the neural responses elicited in the visual cortex by stimuli that possess either or both of the attended features. Most importantly, the attended conjunction stimulus elicited the largest response, with an amplitude approximating the sum of the individual feature enhancements. This electrophysiological evidence for parallel, additive feature enhancement corresponds precisely to the neural mechanism proposed by guided-search theories [4–6]. Specifically, guided-search models account for the increased salience and rapid localization of feature-conjunction targets by proposing that the sensory representations of stimuli with each of the relevant target features are facilitated independently by attention to form parallel feature-activation maps, which are then combined additively to form a single activation map. Target items that possess both features will be doubly facilitated and hence stand out from the distractors on the activation map.

The behavioral and electrophysiological results allow us to rule out the possibility that subjects were attending to stimuli on the basis of flicker frequency rather than their color and orientation features. The findings that both false-alarm rates and SSVEP amplitudes were larger for stimuli with one attended feature than for those with neither attended feature indicate that attention was directed on the basis of the relevant features rather than flicker frequency. Moreover, we previously showed that differences in flicker frequency were not used as a basis for attention when color features were available [11]. We can also reject the possibility that subjects were switching attention between the two features rather than attending to them in parallel. If switching were taking place, the SSVEP amplitudes driven by the c^+o^- and c^-o^+ stimuli would be negatively correlated over time as attention switched from the c^+ to the o^+ feature and back again. In fact, this correlation was found not to differ significantly from zero (see Figure S1 and the Supplemental Experimental Procedures, available online), consistent with our conclusion that the two relevant features were being attended in parallel.

Neurophysiological studies in monkeys [14–18] and fMRI studies in humans [19, 20] and evoked-potential recordings [11] have demonstrated that paying attention to a particular visual feature produces a global increase in gain or amplification of cortical neurons that are responsive to that feature. Such findings have given rise to the feature-similarity gain model [16, 17, 21], which specifies that paying attention to a nonspatial feature such as color or movement direction produces an overall increase in sensory gain for neurons in the visual pathways that prefer that feature throughout the

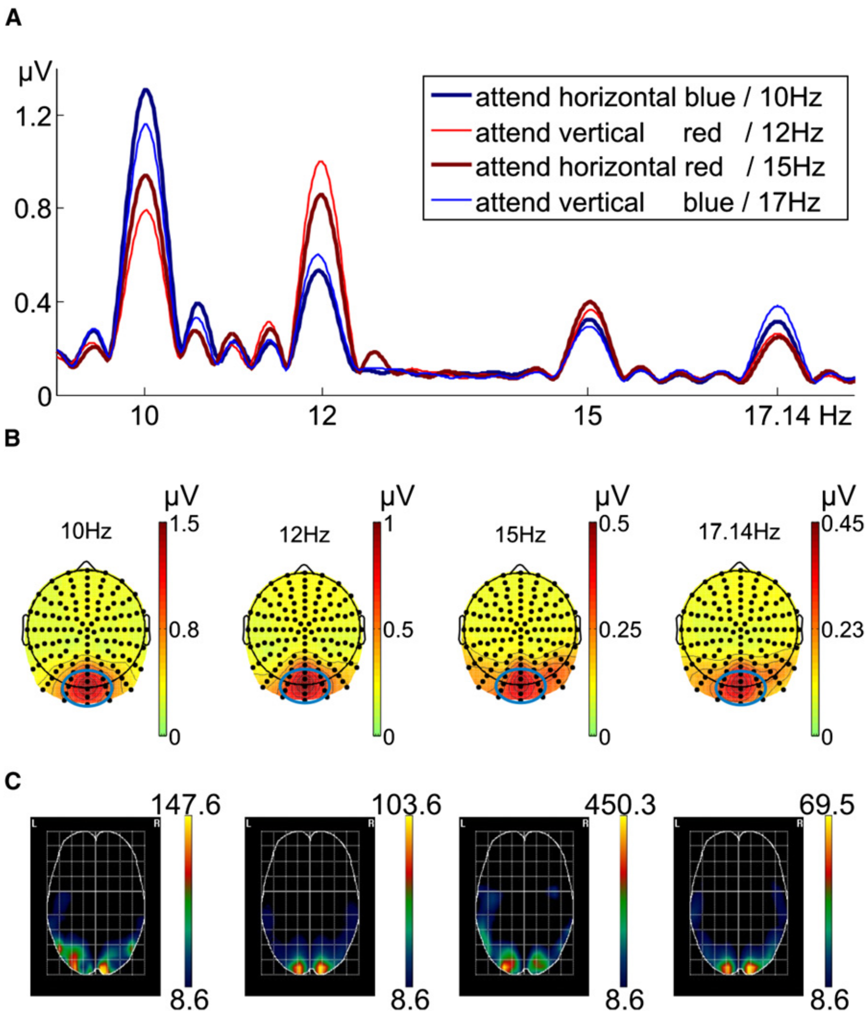

Figure 2. Power Spectrum and Sources of SSVEP

(A) Grand-average power spectrum obtained by fast Fourier analysis of SSVEP waveforms for all four attention conditions averaged across 11 occipital electrodes surrounding electrode Oz. Each peak corresponds to the respective stimulation frequency.

(B) Spline-interpolated voltage maps of SSVEP amplitudes for each stimulation frequency averaged across all experimental conditions. Blue lines indicate cluster of 11 occipital electrodes surrounding Oz.

(C) Statistical parametric maps of the cortical current-density distributions giving rise to the SSVEP amplitude increases for attended versus unattended bars (c^+o^+ minus c^-o^-) for each type of stimulus. Scale represents t^2 values, and the $p < 0.001$ threshold for the attended versus unattended comparison corresponds to 8.56. Thresholds were corrected for multiple comparisons.

visual field. Although these physiological data are consistent with the present findings and with the premises of guided-search models, the previous studies did not compare the effects of attention on neural responses to stimuli with both, one, or neither of the features of attended conjunction stimuli. Hence, these earlier studies could not address the question of whether the multiple features of attended conjunction stimuli are enhanced additively and in parallel, as was done in the present study.

Many questions remain about the mechanisms by which this parallel feature amplification is implemented in the brain. A likely hypothesis is that top-down influences originating from frontal and/or parietal control areas produce an excitatory bias and competitive advantage in neurons that encode the attended-feature value(s) [16, 22, 23]. Remarkably, this biasing appears to occur in visual cortical areas representing much, if not all, of the visual field. The present results suggest that this top-down control is executed early in visual processing, in the cortical region that includes areas V1, V2, and V3. It is not clear, however, whether the bias signals go directly to those areas or are fed back from higher visual areas such as V4 and IT. In any case, the attentional biasing in the present design appears to be feature selective rather than object selective (i.e., selective for the c^+o^+ conjunction), given that the conjunction-specific SSVEP amplification was the simple sum of the individual feature amplifications.

The present findings are consistent with the biased-competition model [23] as well as with the feature-similarity gain model [16, 18, 24], which postulates that paying attention to a particular nonspatial feature produces a global increase in sensory gain for neurons preferring that feature. The present study provides critical new evidence that these gain increases are additive when attended targets are defined by multiple nonspatial features, in accordance with the tenets of guided-search theory [4–6]. This additive feature enhancement gives attended conjunction targets a stronger sensory signal in the visual cortex; this stronger signal enables both rapid localization and continued tracking of those targets against the background of distractors. This mechanism can play a broader role in nonsearch contexts, as exemplified in the present experiment, by making attended multifeature objects stand out perceptually from the background of confusable distractors.

Experimental Procedures

Participants

Fifteen subjects (nine female, three left-handed, mean age 24.8 yr) with normal color vision participated.

Stimuli

Red and blue bar stimuli were presented in a circular display (diameter = 12.9°) on a video monitor against a gray background (Figure 1). Equiluminance of bars and background (fixed at 5.8 cd/m^2) was established for each subject by heterochromatic flicker photometry. Each of the four types of bars (red or blue and horizontal or vertical) flickered at a different rate. Each bar subtended 0.61° × 0.16° and moved 0.51° in a random direction after each screen refresh (rate = 120 Hz).

Procedure

Each trial began with a cue indicating the attended bar type, which was randomized across trials. After cue offset, the display of 300 flickering bars was presented for 3092 ms and was followed by an intertrial interval of 900 ms. The subject's task was to detect occasional 500 ms periods of coherent motion of the attended bars in one of the cardinal directions (targets) while

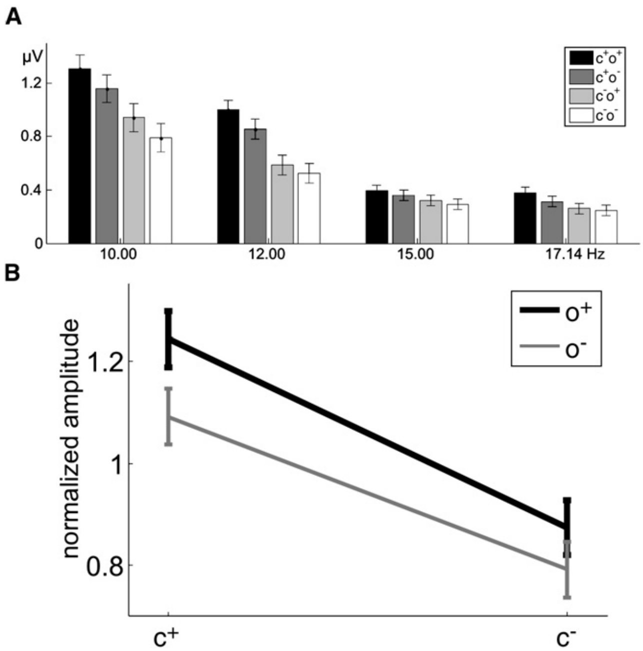

Figure 3. Grand Average SSVEP Amplitudes and Attention Effects

(A) Mean SSVEP amplitudes averaged across 11 occipital electrodes and all subjects for each type of stimulus and attention condition (c^+o^+, color and orientation attended; c^+o^-, color attended and orientation unattended; c^-o^+, color unattended and orientation attended; c^-o^-, color and orientation unattended).

(B) Interaction plot for normalized SSVEP amplitudes averaged across stimulation frequencies when color was attended (c^+, left) or unattended (c^-, right) and when orientation was attended (o^+, bold black line) or unattended (o^-, gray line). Error bars correspond to 95% within-subject confidence intervals.

ignoring similar motions of the other three bar populations (distractors). Only 70% of the dots moved coherently to prevent tracking of single bars. Detection responses made between 300 and 1000 ms after targets or distractors were considered hits and false alarms, respectively.

SSVEP Recordings and Analysis

Brain electrical activity was recorded from 128 electrodes mounted in an elastic cap. On each artifact-free trial with no targets or distractors, SSVEPs were extracted separately for each type of stimulus on the basis of its flicker frequency. SSVEP amplitudes were quantified by Fourier analysis over the interval 400–2800 ms after display onset, normalized by dividing the amplitude at each frequency by the mean amplitude over all attention conditions for that frequency, and compared by repeated-measures ANOVA with factors of attended color (c^+ versus c^-) and attended orientation (o^+ versus o^-).

Supplemental Data

Correlation analysis and one figure are available at http://www.current-biology.com/cgi/content/full/18/13/1006/DC1/.

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